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The enigmatic Namibian egg-eating snake *Dasypeltis loveridgei* Mertens, 1954 (Squamata: Colubridae): A valid species recovered from synonymy

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Abstract. A subspecies of egg-eating snake, *Dasypeltis scabra loveridgei* Mertens, 1954, from Namibia, has been considered a junior synonym of *Dasypeltis scabra* (Linnaeus, 1758) by most authors since 1983. A detailed morphological analysis of 153 preserved museum specimens from Namibia was conducted in order to re-evaluate the taxonomic status of egg-eaters in the country. Two distinct morphotypes, ‘scabra’ and ‘loveridgei’, were identified. In Namibia, *Dasypeltis loveridgei* is typically distinguished from *D. scabra* as follows: mid-dorsal saddles in the form of dark brown hourglass-shaped markings (versus quadrants, ovals or irregular shapes); belly with a single row of dark markings at the edges (versus 2–3 rows or heavily marked); six supralabials on either side of head, 2nd and 3rd in contact with the orbital (versus 7 [3,4]); internasals longer (versus shorter) than the prefrontals; top of rostral barely visible when head is viewed from above (versus clearly visible); frontal often smooth to moderately pitted (versus usually largely to extensively pitted); inter-prefrontal sulcus weakly marked or moderate (versus often deep and distinct). *Dasypeltis scabra* occurs in central and north-eastern Namibia, with a single record in the south-west which may be associated with populations in the Northern Cape Province of South Africa; *D. loveridgei*, which is here shown to be a valid species, is widespread in the country, excluding the north-east, but largely restricted to areas above 1000 m a.s.l. The two species are sympatric at a few localities in central Namibia, and parapatric in several areas throughout the country.

Key words. Serpentes, Colubrinae, *Dasypeltis*, egg-eating snake, taxonomy, Namibia.

INTRODUCTION

The 17 recognised species of egg-eating snakes, *Dasypeltis* Wagler, 1830, are widely distributed in Africa (excluding most of the Sahara) – including isolated populations at Fayum in Egypt, in Morocco and Western Sahara, and in Sudan – and in the western parts of the Arabian Peninsula (Bates & Broadley 2018; Escoriza 2012; Gans 1959, 1964; Saleh & Sarhan 2016; Trape & Mané 2006; Trape et al. 2012, 2021; Uetz et al. 2022). Currently, most authors recognise only three species in southern Africa, namely *Dasypeltis scabra* (Linnaeus, 1758), *Dasypeltis inornata* A. Smith, 1849, and *Dasypeltis medici* (Bianconi, 1859) (Bates et al. 2014; Branch 1998; Broadley 1990; Marais 2004, 2022), with only *D. scabra* recorded from Namibia.

Werner (1902) examined material from Windhoek and was the first author to note that in Namibia, *Dasypeltis* may have a similar dorsal pattern to that of the dwarf adder *Bitis caudalis* (A. Smith, 1839). Sternfeld (1908, 1910a–c) discussed the colour pattern of such Namibian egg-eaters in more detail and considered them to be mimics of *B. caudalis*. More than forty years later, Mertens

(1954) described *Dasypeltis scabra loveridgei* based on a series of 10 specimens from central Namibia. He differentiated it from typical *D. scabra* by the hourglass-shaped dorsal markings along the middle of the back (similar to *B. caudalis*), and also suggested that it had greater numbers of ventral scales (212–218 in males, 225–230 in females).

In his revision of the genus *Dasypeltis*, Gans (1959) examined the paratypes of *D. s. loveridgei* and acknowledged their distinctive dorsal markings, referring to this pattern as ‘6N’. He added that high frequencies of the supralabial formula 6 [2,3] (i.e., six supralabials on either side of head, with 2nd and 3rd in contact with the orbital) occurred in southern Namibia, but that this became less common progressively northwards in the country. Gans (1959) also noted that ventral counts for ‘loveridgei’ were included within the range of variation of *D. scabra*, and he therefore referred *D. s. loveridgei* to its synonymy.

FitzSimons (1962) subsequently recognised *D. s. loveridgei* from the central highlands of Namibia (his record for Tsumkwe in the north-east is referable to *D. scabra*, see below) and noted that although it was indistinguishable from *D. s. scabra* in southern Africa with regards

to scalation, it differed markedly in terms of its colour pattern, most especially its possession of 42–54 hourglass-shaped markings on the back from nape to vent (usually squarish to rhomboical markings in *D. s. scabra*), with rectangular markings on the flanks (usually irregular vertical bars or stripes in *D. s. scabra*), and uniformly white underparts (often with dark spots in *D. s. scabra*). He also noted that *D. s. loveridgei* was apparently a smaller form, the longest known specimen measuring 663 mm in total length (585 mm snout-to-vent + 78 mm tail length); and that it had been suggested that (p. 180) “...tail length [of *loveridgei*] is on average shorter than in typical *scabra*, but this is open to some doubt and remains to be proved by measurements of a long series of correctly sexed specimens.” FitzSimons (1962, 1966, 1970, 1974) did in fact, apart from colour pattern, use relative tail length to separate the two subspecies, i.e., total length/tail length: 5.3–6.8 in *D. s. scabra* and >7 in *D. s. loveridgei*.

For his revision of *FitzSimons’ Snakes of Southern Africa*, Broadley (1983) examined 56 specimens of *Dasypeltis* from Namibia. He noted that specimens with the ‘loveridgei’ pattern and those with a pattern intermediate between this and the typical *D. scabra* pattern varied considerably with regards to colour pattern, ground colour (between the dark markings), ventral counts, subcaudal counts, and upper labial formula (see below), but “there was no correlation between these characters” (p. 265). He added that: “Recognition of *D. scabra loveridgei* as a formal subspecies is not justified, it is better treated as a colour phase, apparently developed in mimicry of *Bitis caudalis*.”

As part of a revision of the genus *Dasypeltis* in the southern half of Africa, data from a sample of 153 Namibian specimens was analysed. Most specimens with mainly ‘hourglass’ markings on the back also had the supralabial formula 6 [2,3] (usually 7 [3,4] in *D. scabra*), which led me to question Broadley’s (1983, 1990) decision to relegate *D. s. loveridgei* to the synonymy of *D. scabra*. Apart from dorsal colour pattern and the supralabial formula, several additional characters were also examined, some of which also proved useful in distinguishing between the two morphotypes.

Bates & Broadley (2018) proposed elevating *D. s. loveridgei* to full species status based on a combination of the unique dorsal colour pattern and usual supralabial formula of 6 [2,3] of several Namibian specimens as determined by Mertens (1954, 1955) and Gans (1959); and they also included Namibia in the distribution range of *D. scabra*. *Dasypeltis loveridgei* was until recently listed as a subspecies of *D. scabra* by The Reptile Database (Uetz et al. 2022). The present study provides data supporting the proposal that *D. loveridgei* is a valid species, and shows that this species and *D. scabra* are both fairly widespread in Namibia.

MATERIALS AND METHODS

Study area

Namibia is a largely arid country in south-western Africa situated between latitudes 16° 45’ and 29° S, and lying mostly to the west of longitude 21° E, although it also includes the relatively narrow north-eastwardly extension known as the Zambezi Region (formerly Caprivi Strip). Although much of the country is arid, including the Namib Desert in the west and the western edge of the Kalahari Desert in the east, the north-easterly parts (especially the Kavango-Caprivi region) are subtropical, receive much more rainfall, and comprise forested savannah and woodland (Anon 2022). Much of the rest of the country consists of some form of savannah or shrubland. The Great Escarpment, including the Khomas Highland in the Windhoek region, runs north to south in the country and separates the western coastal areas (Namib) from the central plateau.

Material examined

Data on size, colour pattern and scalation for a total of 153 specimens of Namibian *Dasypeltis* and for comparison, eight *Dasypeltis confusa* Trape & Mané, 2006 (identification based on data in Trape & Mané 2006, Bates & Broadley 2018 and Trape et al. 2021) from Angola and south-western Democratic Republic of the Congo, from museums in southern Africa, Europe and the United States are presented in Appendix I. This includes data from material examined by the author (values in bold in Appendix I); as well as data from Mertens (1954, holotype: museum number marked by superscripted ‘1’ in Appendix I), Gans (1959, appendix 1: superscripted ‘2’ in Appendix I) and spreadsheets sent by the late Donald G. Broadley (some of this data, recorded using the same methods as in the present study, was probably used for the conclusions reached by Broadley 1983: superscripted ‘3’ in Appendix I). Several of the above-mentioned specimens were examined by the author for at least some characters, and such data is also denoted in bold in the appendix. In some cases the author’s data differs from that presented by Mertens (1954) and Gans (1959). For the holotype and most of the paratypes of *D. s. loveridgei*, as well as six *Dasypeltis* specimens in the Field Museum of Natural History (excluding FMNH 77610), photographic images were examined and data obtained in this way is also indicated in bold in Appendix I. Unless otherwise indicated, when museum specimen numbers are separated by an en dash, this implies a series (e.g., TMP 48337–9 refers to specimens 48337, 48338 and 48339).

Specimens were examined under a binocular dissecting microscope, or with the aid of magnifying lenses for some large specimens (D.G. Broadley, pers. comm.). One decapitated specimen (NMWN 3189b: Ja Dennoch, Kehoro Suid) could not be identified to species level because too few diagnostic characters were available. In

the species accounts, localities (with museum specimen numbers) are listed alphabetically, and the mapping notation (e.g., 2616CB) refers to quarter-degree units (see usage in Bates et al. 2014: 8). Specimens listed as '*Dasypeltis* cf. *loveridgei*', although similar to *D. loveridgei*, were not included in the analysis as their taxonomic status is uncertain and currently under investigation (Bates et al. in prep.), but their localities were mapped.

Because of known differences in numbers of ventral and subcaudal scales between males and females of *Dasypeltis* (e.g., Bates & Broadley 2018; Broadley 1983, 1990; Gans 1959), an attempt was made to determine the sex of all specimens. Sex was determined by presence/absence of (one or both) inverted hemipenes (slit open to reveal spines if not obvious) in the tail base, presence of everted hemipenes, and/or presence of internal reproductive structures (males: testes, sperm ducts; females: eggs, ovaries, oviducts). Only sexed specimens were used for the analyses of relative tail length, and numbers of ventrals, subcaudals and midbody scales.

Characters used

Characters mentioned by previous workers (Broadley 1983; FitzSimons 1962; Gans 1959; Mertens 1954), including all those regarding differences or similarities between *D. scabra* and *D. loveridgei*, were examined and evaluated, together with a few additional characters (see Appendix I). Firstly, the dorsal, lateral and ventral colour patterns were determined. Dorsal pattern was usually identified as '5N' (*scabra*-like) or '6N' (*loveridgei*-like) with reference to Gans (1959), but variation in this regard is discussed. Lateral markings were generally categorised as elongate (typical for *D. scabra*), or squarish or irregular (not distinctly elongate; typical of *D. loveridgei*). Colour pattern on the belly (white to cream) was recorded as immaculate; with one, two or three rows of dark markings at the sides of the belly (not all ventral plates were necessarily marked, and if a single row was present then the markings were at the extreme edges of the plates adjacent to the lateral scales); or extensively marked. The rows of dark markings sometimes extended onto the tail.

Ventrals were counted from the first plate following the posterior (usually second) pair of chin shields, up to but excluding the anal plate (first ventral is always wider than long and usually similar to the next ventral; small extranumerary scales sandwiched between posterior chin shields were not included). Subcaudals were counted from the first adjoining pair behind the vent up to the pair in contact with the terminal spine (spine excluded). Longitudinal dorsal scale rows ('midbody scale rows') were counted at or near midbody (halfway between tip of snout and vent), usually by starting the count caudad and reversing in the same way at the dorsal ridge (vertebral area), but taking special care to follow the inclination of the lateral rows (usually 3–4) of serrated and reduced

scales so as to include them in the count. Pattern cycles refers to the number of moderate to large dark markings ('saddles') on the back, starting after the first (often chevron) marking on the nape (which often extends onto the back of the head) up to the marking above the vent (in cases of bilateral asymmetry, fusion of dorsal markings, or when such dorsal markings were unclear, then lateral bars were used as guiding criteria). For specimens examined by the author, the latter four counts were usually repeated for accuracy. Scale counts on the head were taken on both sides and when different, this was indicated (see Appendix I). For the sake of calculations, in the few cases where counts were available for one side of the head only, it was considered that the counts were equivalent on the other side. Supralabials are expressed as a formula, for example, 7 [3,4], where the numbers in brackets refer to the labials (i.e., 3rd and 4th) in contact with the orbital. The most posterior labial is a large scale at the corner of the mouth.

Apart from the characters mentioned above, the following four additional features were also examined as they were found to be useful in separating the two taxa: i) Texture of the frontal scale (see usage by Bates & Broadley 2018), scored as: 0 = smooth, no pitting; 1 = a single row of pits on the posterior and lateral margins of the frontal; 2 = more extensive marginal pitting (Gans 1959: fig. 2B); 3 = extensive pitting, but with centre of frontal still smooth (Gans 1959: fig. 2A); 4 = entire frontal pitted and center of shield often rugose or corrugated. ii) Depth of the sulcus between the pair of prefrontal scales, scored as: deep or groove-like ('Y' in Appendix I), moderate ('F'), or weak with scales merely in contact ('N'), as illustrated by Gans (1959: fig. 6). iii) Relative length of prefrontal and internasal scales, determined by visual examination. iv) Protrusion of the top of the rostral scale when viewed from directly above the head, i.e., clearly visible or barely visible (only the tip of the scale is evident).

Snout-vent length (SVL; tip of snout to vent) and tail length (vent to tip of tail) were measured (usually belly-up) with the snake aligned against a millimetre ruler, but a few tightly curled specimens were measured using a length of string. Relative tail length (e.g., total length/tail length) was determined using these measurements. Measurements of truncated tails were not included in calculations.

Statistical analyses

Statistical analyses were conducted using the computer software package Statistica ver. 6. To test whether specimens assigned to the three species on the basis of their dorsal patterns ('5N' for *D. scabra*, '6N' for *D. loveridgei* and '5L' for *D. confusa*) could also be distinguished by morphological characters, a stepwise discriminant function analysis was conducted for all specimens with full sets of the relevant variables (as defined above). For

D. scabra, two specimens (JV 95149, NMWN 2287) had the ‘6N’ pattern, and one (NMWN 9510) had a ‘7’ (*D. palmarum*-like, see Gans 1959) pattern, whereas for *D. loveridgei* one (JV 7340) was ‘5N’ and two (TM 33499, 49876) were intermediate (5N/6N in Appendix I); these six specimens were excluded from the analysis. Thirteen variables were analysed – meristic: numbers of ventrals; subcaudals; midbody scale rows; supralabials (for this variable and the following four, an average was used if different on either side of the head); preoculars; postoculars; anterior temporals; posterior temporals; and interval variables: frontal (scored as noted above, from 0 for smooth to 4 for extensively pitted; in a few cases where Gans [1959] had scored the frontal as ‘Y’ [‘3/4’ in Appendix I, meaning extensively pitted] a score of 3.5 was assigned, or ‘N’ [‘1/2’ in Appendix I, meaning marginally pitted] a score of 1.5 was assigned); length of prefrontal scale compared to internasal (coded as 0 if prefrontal was longest, 1 if they were equal, and 2 if the internasal was longest; score averaged if different on either side); prominence of the posterior part of the rostral when looking down on the head (0 if barely visible, 1 if clearly visible); depth of inter-prefrontal sulcus (0 if weakly marked, 1 if moderately marked and 2 if deep); and the ratio total length/tail length.

Comparative data used in diagnosis

In addition to data in this paper, comparative data for the diagnosis of *D. loveridgei* (see below) and comparison with other species was obtained from Bates (2013), Bates & Broadley (2018), Bates & Ineich (2012), Broadley (1990), Duméril et al. (1854), FitzSimons (1962), Gans (1959, 1964), Mertens (1954, 1955), Saleh & Sarhan (2016), Trape & Mané (2006), and Trape et al. (2012, 2021). For *D. atra*, to avoid inadvertently including data for mainly brown or uniform phase specimens of congeners, only data from north-east Africa (Bates & Broadley 2018) and eastern Democratic Republic of the Congo (Mount Kabobo and the ‘districts’ of Oriental and Kivu: Gans 1959, appendix 1) with ‘2M’, ‘2B’ and ‘2Bx’ dorsal colour patterns were used. An exceptionally low female subcaudal count of 50 for *D. gansi* (see Bates & Ineich 2012), and low male ventral and subcaudal counts of 212 and 59 respectively for *D. fasciata* (see Bates & Broadley 2018), were excluded, as were high ventral and low subcaudal counts of 250 and 55 respectively for a ‘male’ *D. bazi* (Saleh & Sarhan 2016).

Institutional abbreviations

Material (including colour photographs) from the institutions listed below was examined. Institutional abbreviations are from Sabaj (2016).

CAS	= California Academy of Sciences, San Francisco, USA
FMNH	= Field Museum of Natural History, Zoology Department, Chicago, USA

JV	= John Visser collection (to be accessioned into National Museum, Bloemfontein, South Africa)
MCZ	= Museum of Comparative Zoology, Harvard University, Cambridge, USA
MRAC	= Musée Royal de l’Afrique Centrale, Tervuren, Belgium
NHMUK	= Natural History Museum, London, UK
NMW	= Naturhistorisches Museum, Wien [Vienna], Austria
NMWN	= National Museum of Namibia, Windhoek, Namibia
NMZB	= Natural History Museum of Zimbabwe, Bulawayo, Zimbabwe
SMF	= Senckenberg Naturmuseum, Frankfurt am Main, Germany
TMP	= Ditsong National Museum of Natural History, Pretoria, South Africa
ZFMK	= Zoologisches Forschungsmuseum Alexander Koenig, Bonn, Germany
ZMB	= Museum für Naturkunde, Berlin, Germany
ZMH	= Zoological Museum Hamburg, Germany
ZSM	= Zoologische Staatssammlung München, Munich, Germany

Species concept and species delimitation

A lineage-based species concept is followed here, where a species is represented by an independently evolving metapopulation lineage (see De Queiroz 1998, 2007; Frost & Hillis 1990). Morphological characters were the operational criteria for species delimitation.

SYSTEMATICS

Dasypeltis scabra (Linnaeus, 1758)

English: Common Egg-eater; Afrikaans: Gewone Eiervreter; German: Gewöhnlicher Eierfresser

Coluber scaber Linnaeus, 1758: 223. Type locality: ‘in Indiis’ [= Cape Colony, South Africa].

Dasypeltis scabra Gans 1959: 141 (part, app. 1: specimens with ‘5N’ colour pattern, and the following specimens with ‘6N’ pattern: FMNH 64563, 64682, 65853–4, HM 5796 [= ZMH R02271] and MCZ 39930; see Appendix I); Broadley 1983: 262 (part), 1990: 262 (part); Marais 1985: 92 (part); Branch 1988: 84 (part), 1998: 95 (part); Marais 1992: 172 (part), 2004: 270 (part), 2022: 311 (part); Schleicher 2015: 187 (part), 2018: 187 (part), 2020: 198 (part).

Dasypeltis scabra loveridgei Mertens, 1954: 213 (part, Okahandja: SMF 46371; see Discussion).

Dasypeltis scabra loveridgei (not Mertens) FitzSimons 1962: 179 (part, Tsumkwe only); ? Elzen 1980: 337 (Okaukuejo).

Dasypeltis “*scabra*” Göthel, 2015a: 19 (part).

Description. *Colour pattern* (Figs 1–2): Dorsum usually grey or light brown with dark brown to blackish markings (sometimes white-edged) in the form of saddles (41–66, mean 51.7 ± 4.83 , $n = 47$) that vary in shape from square to somewhat rectangular, oval (e.g., TM 55505), irregular (e.g., CAS 196434), and often a mixture of two or more shapes; and vertically elongated markings of the same colour (sometimes white-edged) on the flanks situated between, and mostly separated from, the saddles (‘5N’ pattern of Gans 1959). The spaces between saddles are usually whitish and shorter (and smaller) than the saddles themselves. Occasionally the dorsal pattern is closest to ‘6N’ (JV 95149, Katima Mulilo), or the saddles are somewhat intermediate, being squarish and only weakly constricted anteriorly and posteriorly (e.g., FMNH 65853, NMWN 2287 and ZMH R02272; also compare Figs 1–2 ‘*scabra*’ and Fig. 8 ‘*loveridgei*’). Lateral markings are also variable and may be similar in this species and *D. loveridgei* (e.g., Figs 1, 9). In a few specimens some of the saddles and lateral markings are confluent, but NMWN 9510 (Waterberg) is unusual in that it has almost *D. palmarum*-like markings (colour pattern ‘7’ of Gans 1959), with elongate to diamond-shaped saddles mostly linked to the lateral bars, forming bands. Venter white to cream, seldom immaculate (NMWN 9228, 9510; TM 22612), usually with grey stipples or dark blotches at the edges, occasionally forming a single row (TM 83351) on either side of the belly, but 2–3 well-spaced rows on either side or belly extensively marked in 84.6% (two rows on either side in 57.7%, three rows in FMNH 65854, and two rows with additional dark markings elsewhere on the belly in 23.1% – e.g., TM 39329 and 44799 which have extensively marked bellies) ($n = 26$). Top of head usually with 1–2 anterior-pointing (sometimes fragmentary) chevrons and/or other dark markings.

Scalation (Figs 3–4): Dorsal (including lateral) scales distinctly keeled; usually 3–4 (occasionally 0 or 5) rows of lateral scales keeled and serrated ($n = 49$). In most specimens, scales of the 3th to 5th or 3rd to 6th rows from the ventral plates were serrated, but exceptions were 2nd to 6th rows (TM 55505), 3rd to 7th rows (TM 22612) and 4th to 6th rows (NMWN 9228) serrated, while juveniles NMWN 204 (202 mm SVL) and NMWN 9510 (149 mm SVL) lacked serrated laterals ($n = 31$). Preoculars usually one on either side of head, but two on either side in NMWN 4398 ($n = 48$); postoculars usually two on either side of head, but one on either side in ZMH R02272 ($n = 48$). Frontal shield heavily pitted (States 3 or 4) in 76.6% of specimens, marginally pitted (States 1 or 2) in 23.4% ($n = 47$). Inter-prefrontal suture deeply sunken in 68.1% of specimens, moderately marked in 29.8%, weakly

marked in juvenile NMWN 9228 ($n = 47$). Supralabials 7 [3rd and 4th entering orbit] on either side of head in 85.7% of specimens, 6 [2,3] in 4.1%, 6 [2,3] on one side and 7 [3,4] on the other in 4.1%, and individuals with 6 [3] (NMWN 204), 7 [2,3,4] (JV 95003), and 8 [4,5] / 7 [3,4] (NMWN 4397) ($n = 49$). Temporal formula on either side of head usually 2 (anterior) + 3 (posterior) or 3+4: anterior temporals usually two on either side of head (66.7%), sometimes three (20.8%), occasionally 3 left/2 right (10.4%), and 3/4 in NMWN 7082 ($n = 48$); posterior temporals on either side of head three (54.2%), three on one side and four on the other (25.0%), four (16.7%), and individuals with two (NMWN 9510) and 3/5 (NMWN 3189a) ($n = 48$). Nasal shield usually semi-divided (i.e., suture present between nostril and first supralabial), but fully divided (suture present above and below nostril) in NMWN 4398, and undivided on left side of head and semi-divided on right in TM 39328 ($n = 41$). Prefrontal scales longer (and usually larger overall) than internasals in 90.5% of specimens, internasals longer in 4.8%, of equal length in JV 95001, and prefrontal longer on left side, equal on right, in TM 39329 ($n = 42$). When the head is viewed from above, the top of the rostral shield is visible and distinct in all but one specimen (TM 55505) in which it is barely visible ($n = 42$). Midbody scale rows 22–28 ($n = 49$), in males 22–26 (mean 24.1 ± 1.28 , $n = 15$), in females 23–28 (mean 24.8 ± 1.15 , $n = 23$). Ventrals 204–240 ($n = 46$), in males 204–220 (mean 210.0 ± 4.36 , $n = 15$), in females 212–240 (mean 224.3 ± 6.72 , $n = 22$). Subcaudals 41–62 ($n = 45$), in males 51–62 (mean 56.6 ± 3.32 , $n = 14$), in females 41–55 (48.3 ± 3.61 , $n = 21$).

Relative tail length: SVL/tail length in males 4.69–5.76 (mean 5.25 ± 0.38 , $n = 14$), in females 5.93–8.12 (mean 7.23 ± 0.66 , $n = 19$); total length/tail length in males 5.69–6.76 (mean 6.25 ± 0.38 , $n = 14$), in females 6.93–9.12 (mean 8.23 ± 0.66 , $n = 19$).

Size. Largest male (TMP 39329 – Katima Mulilo) 467 mm SVL + 98 mm tail length = 565 mm total length; largest female (NMWN 2292 – Witvlei, Gobabis) 730 + 97 = 827 mm, but NMWN 253 (Wilhelmsruhe) had a SVL of 773 (no tail measurement).

Localities and material examined. (Names followed by numbers refer to farms.) Breitenberg 51, Gobabis district – NMWN 2281 (2218DC); Cleveland farm, 9 km N of Otjiwarongo – TMP 83351 (2016BC); Eastern National Water Carrier, Waterberg section – NMWN 9510; Etosha Pan, Kaokoveld – FMNH 77610; Good Hope 397, Gobabis district – NMWN 2293 (2218AB); Grootfontein campground – CAS 196434 (1918CA); Grootfontein-Omatoko Canal, Grootfontein district – NMWN 4924 (1917DD); Hippo 386, Gobabis district – NMWN 2290 (2219AA); Ja Dennoch, Kehoro Suid – NMWN 3189a (2318CA); Kabuta, Katima Mulilo – TMP 22612 (1724DD); Katima Mulilo – NMZB-UM 24208 (1724AC); NMWN 7082, 10133 (1724AD); JV 95149, TMP 39328–9 (1724CB); Katima Mulilo, 15 km WSW



Fig. 1. *Dasypeltis scabra* from Otjiwarongo, northern Namibia. (Photo: Francois Theart)



Fig. 2. Dorsal and ventral aspects of *Dasypeltis scabra* (FMNH 65853) from near Okahandja, central Namibia. (Photos: Field Museum of Natural History, Chicago)

of – NMZB–UM 22810 (1724CA); ‘Namibia’ – FMNH 64682, ZMB 28815; Okahandja – NMWN 204, 2294, SMF 46371, TMP 36071, ZMH R02275 (2116DD); Okahandja, near – FMNH 65853–4 (2116DD); Okahandja district – FMNH 64563; Okakena near Okahandja – ZMH R02272 (2116DD); Onjoka farm, Eastern Na-

tional Water Carrier – NMWN 9228 (2017AD); Otjiwarongo – JV 95001, 95003, 95005 (2016BC); Otjosangombe – MCZ 39930 (2017AD); Outjo, 21 km due NW of – JV 8926 (2015BB); Plateau 38, Luderitz district – TMP 55505 (2616DA); Roidina farm, Omaruru district – ZMH R02271 (2116AA); Tsumkwe – NMWN



Fig. 3. Lateral aspect of the head of *Dasypeltis scabra* (SMF 46371) from Okahandja, north of Windhoek, Namibia, showing typical arrangement of seven supralabials (3rd and 4th in contact with orbital). (Photo: Sebastian Lotzkat)

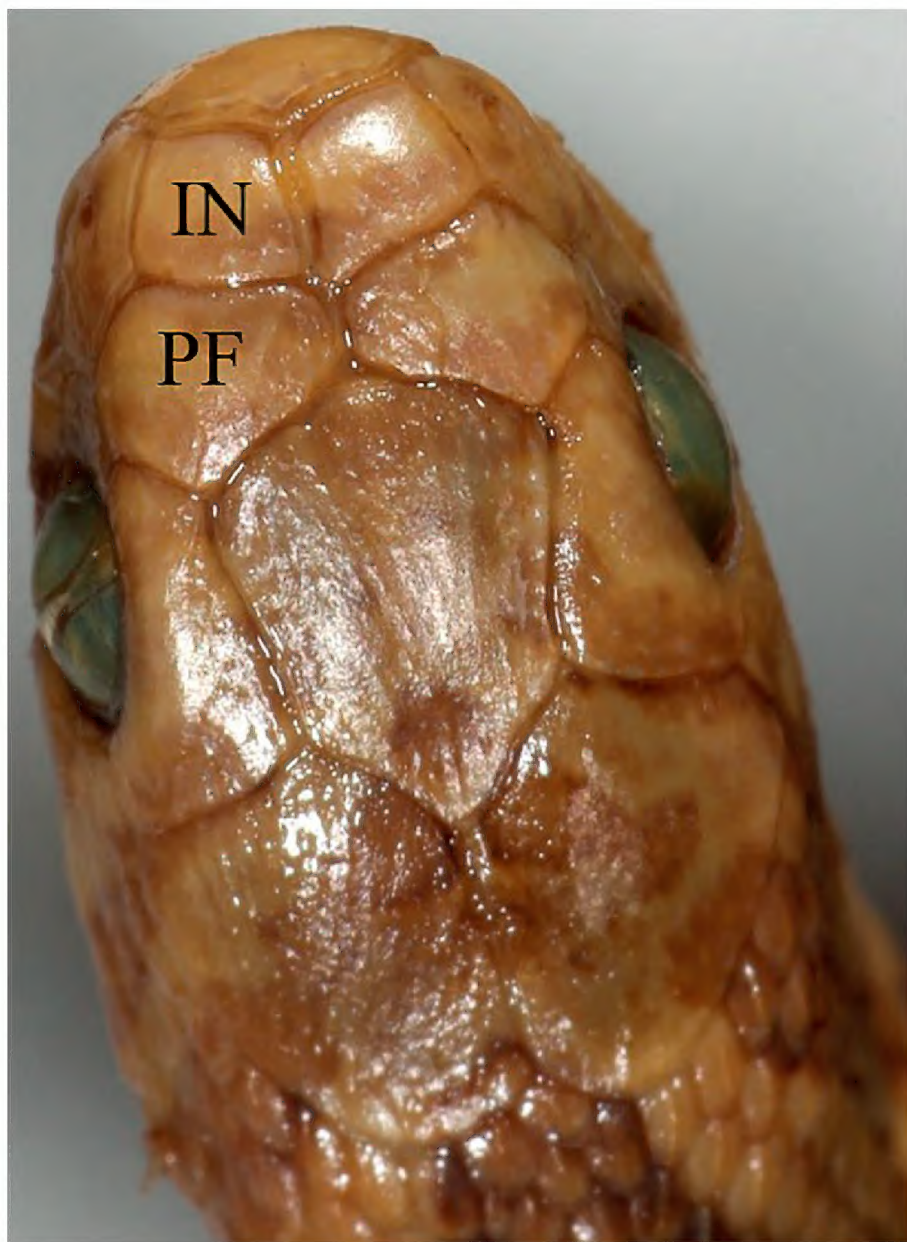


Fig. 4. Dorsal aspect of the head of *Dasypeltis scabra* (SMF 46371) from Okahandja, north of Windhoek, Namibia, showing typical condition of head shields (top of rostral shield clearly evident when viewed from above head; internasals [IN] shorter [and usually smaller overall] than prefrontals [PF]; inter-prefrontal sulcus well marked; and frontal shield extensively pitted [even partly corrugated in this case]). (Photo: Sebastian Lotzkat)

4397–8, 10131, 10135, TMP 25091 (1920DA); Waterberg Plateau – NHMUK 1937.12.3.152–3 (2017AD); Wendelstein 171, Gobabis – TMP 44799–800 (2219AC); Wilhelmsruhe 339, 45.1 km E of Steinhausen – NMWN

253 (2118DC); Windhoek – CAS 115894, NMWN 2287 (2217CA); Witvlei, Gobabis – NMWN 2292 (2118DC).

Distribution. From the south-western Cape of South Africa through Namibia, Botswana, Zambia, southern and western Democratic Republic of the Congo, much of south-eastern and eastern Africa as far north as Gojam area in north-central Ethiopia, with isolated populations along the Nile Valley in south-eastern Sudan and adjacent north-eastern South Sudan, as well as 50 km north of Kutum in western Sudan (Bates & Broadley 2018; Bates et al. 2014; Broadley 1990; Gans 1959).

In Namibia *D. scabra* is found mainly above 1000 m a.s.l., in Woodland and Shrubland-Woodland Mosaic in the north-eastern parts of the country, extending into the higher-lying central parts, with a single record in the south-west which appears to be associated with populations in the Northern Cape Province of South Africa (Fig. 5). Found in the following regions of Namibia: Kunene, Zambezi, Erongo, Otjozondjupa, Omaheke, Khomas, Hardap and Karas.

Conservation. Using IUCN (2022) criteria, this species in Namibia is considered Least Concern as it is widespread and apparently common, and there are no known major threats.

Remarks. Mertens (1955) and Gans (1959) noted that one of the paratypes (SMF 46372, Okahandja) of *D. s. loveridgei* had dorsal markings similar to those of typical *D. scabra*. One of two specimens from this locality does indeed have the ‘5N’ pattern (and other *scabra*-like characteristics), but bears the label SMF 46371 (see Discussion).

Several specimens listed by Gans (1959) as having a ‘6N’ dorsal pattern (hourglass-shaped markings on the back, i.e., *D. loveridgei*-like) are in fact referable to *D. scabra* (see Appendix I). Most of these specimens (FMNH 64563, 64682, 65853–4, HM 5796 [= ZMH R02271]) have a somewhat intermediate dorsal pattern in that some or most of the saddles are roughly square-shaped but moderately constricted anteriorly and posteriorly. However, other characters on these specimens were typical of *D. scabra*: supralabial formula was 7 [3,4], frontals extensively pitted, and belly had at least two rows of dark spots at the edges on either side (the latter character not recorded for the ZMH specimen). Gans (1959, appendix 1) recorded the dorsal pattern of MCZ 39930 as ‘?6N’, but it is referable to *D. scabra* as it has the supralabial formula 7 [3,4] and an extensively pitted frontal.

Dasypeltis loveridgei Mertens, 1954

English: Namibian Egg-eater; Afrikaans: Namibiese Eirvreter; German: Namibischer Eierfresser

Dasypeltis scaber (not Linnaeus) Peters 1870 [dated 1869]: 661 (Damaraland).

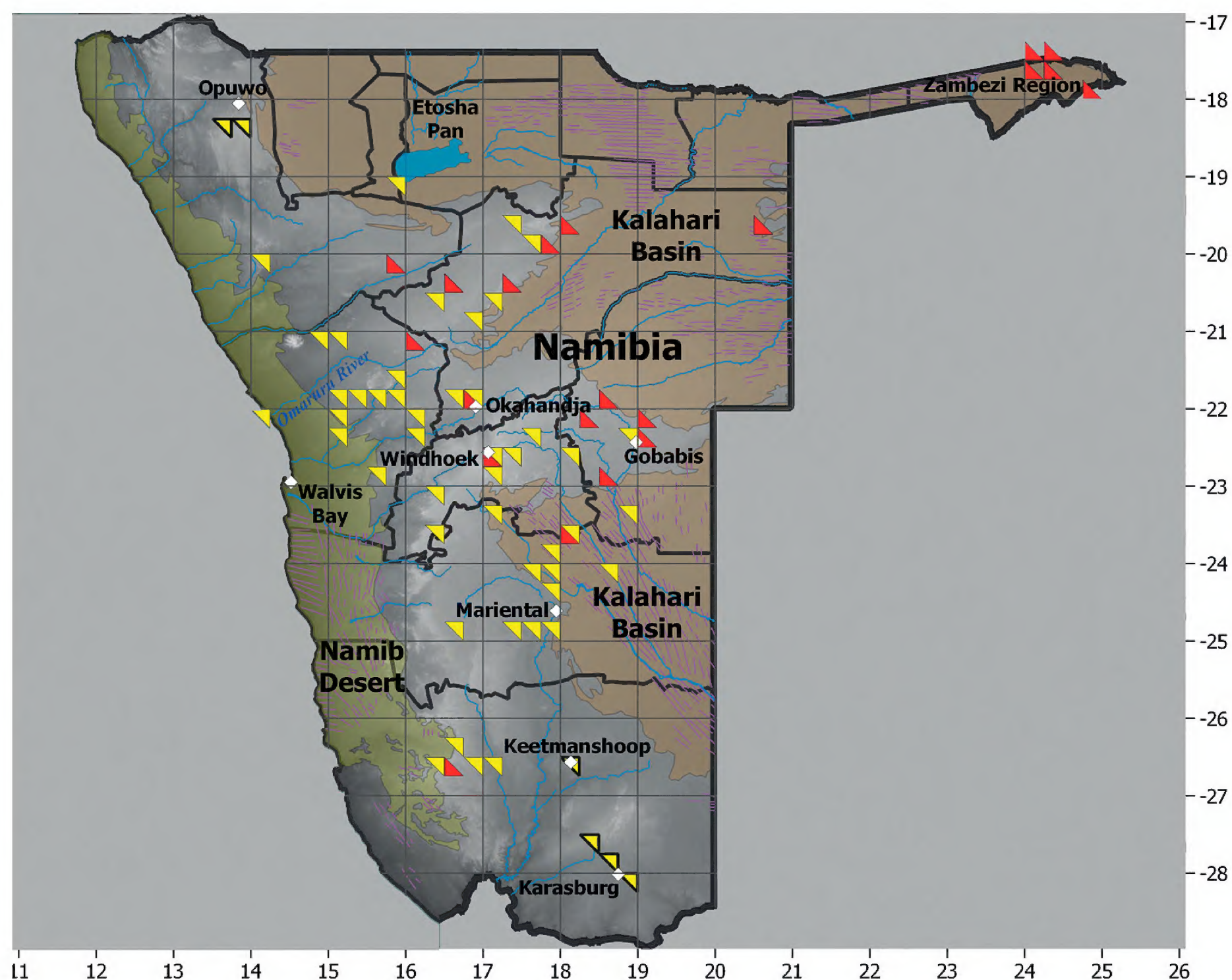


Fig. 5. Geographical distribution of egg-eating snakes (*Dasypeltis*) in Namibia, based on museum material examined for this study. Symbols represent quarter-degree grid cells (see usage in Bates et al. 2014). Red triangles = *D. scabra*, yellow triangles = *D. loveridgei*; yellow triangles with bold edges = *D. cf. loveridgei*. The two species are sympatric at three localities, namely Windhoek, Okavango and Ja Dennoch (quadrants comprised of red and yellow triangles), and parapatric in several areas throughout the country.

(Map produced by Cora S Stobie using QGIS [QGIS Development Team 2020] and Natural Earth [https://naturalearthdata.com]; shapefiles for “Namibia – Kalahari and recent deserts” as well as “Biomes and vegetation types of Namibia” [Mendelsohn et al. 2002] were included for dune, river and basin data [originally available on www.the-eis.com, currently available on www.data.sasscal.org]; subnational administrative boundaries from <https://data.humdata.org/dataset/cod-ab-nam>; Global Multi-resolution Terrain Elevation Data 2010 [GMTED2010] [Danielson & Gesch 2011] was added to provide an elevation layer. Websites last accessed 9 Sep. 2020.)

Dasypeltis scabra (not Linnaeus) Werner 1902: 340 (Windhoek); Sternfeld 1908: 89, 1910a: 55, 1910b: 58, 1910c: 21 (Gobabis & Windhoek); Lampe 1911: 197 (Rietmond); Gans 1959: 141 (part: pl. 8, figs 3,4; pl. 5, fig. 8; and app 1: specimens with ‘6N’ colour pattern, excluding FMNH 64563, 64682, 65853–4, HM 5796 [= ZMH R02271] and MCZ 39930, which are *D. scabra*; see Appendix I); Broadley 1983: 262 (part), 1990: 262 (part); Marais 1985: 92 (part); Branch 1988: 84 (part), 1998: 95 (part); Marais 1992: 172 (part), 2004: 270 (part), 2022: 311 (part); Schleicher 2015: 187 (part), 2018: 187 (part), 2020: 198 (part).

Dasypeltis scabra loveridgei Mertens, 1954: 213. Type locality: Farm Finkelstein near Windhoek, Namibia. Holotype: SMF 46642. (One specimen in the type series, SMF 46371, is referable to *D. scabra*; see Discussion); Mertens 1955: 104 (part, excluding ‘SMF 46372’ [= SMF 46371, see Discussion]); FitzSimons 1962: 179 (part, excluding Tsumkwe), 1966: 55; 1970: 114 (central highlands of Namibia), 1974: 114 (central highlands of Namibia); Elzen 1980: 337 (part, Ombujomatamba; ? Okaukuejo).

Dasypeltis loveridgei Bates et al. 2009: 69; Göthel, 2015a: 14, 19, 21 (as '*D. loveridgei*'), 2015b: 86; Bates & Broadley 2018: 6.

Dasypeltis loveridgei (sic) Marais 2022: 312 ('dry western region of southern Africa').

Revised diagnosis. Assigned to the genus *Dasypeltis* on account of its slender form; possession of (usually) 3–4 rows of reduced, oblique, keeled and serrated lateral scales (little or no serration in *D. inornata*); and head barely distinct from the neck (moderately distinct in *D. fasciata*). Distinguished from congeners by the following combination of characters: 1) Moderate to small size of males (largest: 445 mm SVL + 75 mm tail length) and females (689 + 91 mm respectively). 2) Dorsal surfaces grey, light brown or reddish-brown with a series of 36–65 dark, hourglass-shaped, patches or 'saddles'. 3) Sides of body with squarish to irregular, often vertically-oriented, dark markings (seldom distinctly elongate). 4) Ventral surfaces white to cream, immaculate or (usually) with a single row of small, often indistinct, spots or irregular markings at the edges. 5) Supralabials usually 6 on either side of head, with 2nd and 3rd in contact with the orbital. 6) Midbody scale rows longitudinally 22–25 in males, 23–27 in females. 7) Ventrals 202–226 in males, 212–236 in females. 8) Subcaudals 47–60 in males, 38–50 in females. 9) Postoculars 2 (rarely 3) on either side of head. 10) Frontal shield usually smooth to moderately pitted. 11) Inter-prefrontal sulcus almost always shallow to moderate. 12) Internasal scales usually longer (and often larger overall) than prefrontals. 13) Rostral shield barely visible from above head.

Comparison with other species. The colour pattern as described above is characteristic of *D. loveridgei*, and in this regard it differs from other species of *Dasypeltis*. While some specimens of *D. scabra* in southern Africa (e.g., Alexander & Marais 2007: 130–131; Clauss & Clauss 2002: 79) and *D. bazi* (Bates & Broadley 2018: 20) have a similar pattern, the constriction of the saddle is never as distinct and pronounced as it is in most *D. loveridgei*, and in *D. bazi* most saddles are antero-posteriorly elongated, often quite distinctly. There are 36–65 saddles in *D. loveridgei*, but in some other species this count is often much higher (108–141 in *D. fasciata*, 57–108 in *D. medici*, 65–98 in *D. abyssina*, 62–130 in patterned *D. atra*, 62–79 in *D. arabica*). Regarding the markings on the belly, in *D. loveridgei* it is immaculate or poorly marked by a single (occasionally two) longitudinal series of small dark flecks or spots at the edges of the ventral plates; whereas in *D. abyssina* it is extensively decorated in dark brown to black blotches and spots; in *D. parascabra* it is also more extensively marked, with a series of large, bold, dark markings on either side of each ventral plate, well separated from the edge, forming a pair of broken 'stripes'; in *D. medici* there are often fine grey speckles throughout; in *D. palmarum* there are usu-

ally fine dark speckles at the edges of the plates; and the underparts of *D. inornata* are usually immaculate.

Regarding scalation, the usual supralabial formula of 6 [2,3] distinguishes *D. loveridgei* from all other congeners where the formula is usually 7 [3,4] (although 6 [2,3] on both sides of the head in as much as 49.3% of *D. scabra* [$n = 373$] from Free State Province, central South Africa, based on material in the National Museum [Bloemfontein] collection; M.F. Bates, unpubl. data). Division of the nasal scale below the nostril, as in *D. loveridgei*, is the norm in the genus, but in both *D. sahelensis* and *D. parascabra* this scale is undivided. As in other species, *D. loveridgei* usually has two postocular scales on either side of the head, but specimens in western populations of *D. atra* usually have only one. The frontal shield is usually smooth to moderately pitted in *D. loveridgei* but usually extensively pitted in *D. medici* and some populations of *D. scabra*. Ventral plates in *D. loveridgei* were 202–226 in males, 212–236 in females, generally lower than in *D. arabica* (236–244 males, 239–254 females), *D. abyssina* (226–247 males, 241–271 females), *D. gansi* (221–240 males, 235–255 females), *D. medici* (220–252 males), and *D. fasciata* (225–260 females). Subcaudal counts in *D. loveridgei* were 47–60 in males, 38–50 in females, mostly lower than in *D. inornata* (81–92 males, 69–84 females), *D. fasciata* (71–91 males, 64–84 females), *D. medici* (69–109 males, 61–90 females), *D. palmarum* (68–77 males, 62–77 females), *D. gansi* (68–83 males, 59–73 females), *D. arabica* (63–65 males, 53–61 females), *D. crucifera* (61 male, 49–52 females), *D. bazi* (59–61 males, 50–55 females), *D. abyssina* (57–68 males, 49–65 females), and *D. latericia* (59–72 females).

Dasypeltis loveridgei is similar to *D. scabra* with regard to some scalation characteristics, but can be distinguished from the latter in Namibia as follows: dorsal and ventral colour patterns as described above, smaller size (largest male 445 mm SVL + 75 mm tail length versus 467 + 98 mm; largest female 689 + 91 mm versus 730 + 97 mm [one female had a SVL of 773 mm]); supralabial formula usually 6 [2,3] versus 7 [3,4]; internasal usually longer (and larger) versus shorter (and smaller) than prefrontal; frontal shield usually smooth to moderately pitted versus usually largely to extensively pitted; inter-prefrontal sulcus shallow to moderate versus usually deep and distinct; and rostral usually barely visible from above versus almost always more prominent and easily visible.

Description. *Colour pattern* (Figs 6–9): Dorsal colouration is grey, light brown or reddish-brown, with darker brown, predominantly hourglass-shaped, saddles (36–65, mean 47.3 ± 5.37 , $n = 99$) constricted anteriorly and posteriorly, and usually squarish to elongated lateral markings situated between the saddles and adjacent to the pale interspaces ('6N' pattern of Gans 1959: pl. VIII fig. 4). The interspace between saddles may be as long, or longer, than the saddles themselves (e.g., Figs 6–7, 9;



Fig. 6. *Dasypeltis loveridgei* from Dordabis, south-east of Windhoek, Namibia. (Photo: Francois Theart)

Bates & Broadley 2018: fig. 11), but occasionally much narrower (e.g., Fig. 8). Colouration and pattern in life are quite varied (Figs 6–8). For example, the snake in Fig. 6 is grey overall, with moderate sized, dark grey-brown, distinctly constricted, hourglass-shaped saddles on the back and tail, separated by cream-white interspaces that are about equal in length or slightly longer than the saddles themselves. In this specimen some saddles are greatly constricted, a few even separated into pairs of small spots paravertebrally, and the lateral markings vary from spot-like to elongate. This specimen is similar to the holotype (Fig. 9), although the latter has less strongly-constricted saddles and more elongate markings on the flanks anteriorly. The specimen in Fig. 7 has similar colouration and pattern but the saddles are large and dark brown, the interspaces between saddles are only slightly paler (whitish) than the overall grey colouration, and lateral markings are squarish to irregular in shape, seldom elongated. Figure 8 illustrates a snake with an overall light brown colour, with large, reddish-brown, weakly to moderately constricted, saddles, separated by bright white interspaces much shorter than the saddles themselves, with irregular to slightly elongated reddish-brown lateral markings (see photographs of similar snakes in Gothel 2015a: 14, 21, 2015b: 86). Other specimens with weakly constricted hourglass-shaped markings are JV

7304 (Kuibis), NMWN 2279b (Plateau 38, Luderitz), NMWN 10132 (Nauchas farm, Rehoboth), TM 48338–9 (Waterberg Plateau), and TM 42963 (Mariental). One specimen (JV 7340, near Maltahohe) had mostly the ‘5N’ *D. scabra* pattern, while two (TM 33499 and TM 49876) had a pattern intermediate between ‘6N’ and ‘5N’. Saddles and lateral markings were often fused in NMWN 6883 and NMWN 9567. Venter white to cream, immaculate in SMF 40873 and TM 29834, usually unmarked except for the edges of the plates of which some (usually at least every second ventral) have a small dark stipple or spot, usually near or at the contact point with the lateral scales, forming a weak and often poorly defined row down either side of the belly (93.9% of specimens; a few of these, including the holotype [Fig. 2], NMWN 4509 and 5299 also have fine stippling/shading at the edges of the plates), but a couple of specimens (JV 7344; NMWN 10132) have two such rows (closely spaced), while TM 29834 has only fine stippling/shading and no distinct spots/markings ($n = 66$). Top of head with (e.g., holotype, Fig. 11) or without (e.g., Fig. 8) 1–2 anterior-pointing (sometimes fragmentary) chevrons, as well as other small dark markings.

Scalation (Figs 10–11): Dorsal (including lateral) scales distinctly keeled, and usually 3–4 (occasionally 0–2) rows of lateral scales on the body keeled and ser-



Fig. 7. *Dasypeltis loveridgei* from Klein Spitzkoppe, Erongo Region, Namibia, at the western edge of the species' range. (Photo: Wulf D. Haacke)



Fig. 8. *Dasypeltis loveridgei* offspring from parents collected in Tsumeb, northern Namibia. (Photo: Christian Schneider)



Fig. 9. Dorsal and ventral aspects of the holotype (SMF 46642) of *Dasypeltis loveridgei* Mertens, 1954 from Farm Finkenstein near Windhoek, Namibia. (Photos: Sebastian Lotzkat)

rated ($n = 102$). In most specimens, scales of the 3rd to 5th or 3rd to 6th rows from the ventral plates were serrated, but exceptions were only 4th row serrated (ZMH R02273, 208 mm SVL), 4th to 5th rows serrated (NMWN 1828, 5299), and 4th to 7th rows serrated (ZMB 33670b), while three juveniles (190–225 mm SVL: JV 7304, 8510, 8930) lacked any serrated laterals ($n = 52$). Preoculars usually one on either side of head, but two on left side and one on the right in TM 55690 ($n = 103$); postoculars usually two on either side of head, but three in NMWN 2291,

and three left and two right in NMWN 1463 ($n = 104$). Frontal shield smooth in one specimen (ZMB 20920), marginally pitted (States 1 or 2) in 69.3%, and largely to heavily pitted (States 3 or 4) in 29.7% ($n = 101$). Inter-prefrontal sulcus shallow in 63.7% of specimens, moderately marked in 34.3%, and strongly marked in NMZB 10913 and SMF 41928 ($n = 102$). Supralabials 6 [2nd and 3rd contacting the orbital] on either side of head in 81.6% of specimens, 7 [3,4] in 6.8%, 7 [3,4] on one side and 6 [2,3] on the other in 7.8%, and one individual



Fig. 10. Lateral aspect of the head of the holotype (SMF 46642) of *Dasypeltis loveridgei* Mertens, 1954 from Farm Finkenstein near Windhoek, Namibia, showing typical arrangement of six supralabials (2nd and 3rd in contact with orbital). (Photo: Joseph Vargas)



Fig. 11. Dorsal aspect of the head of the holotype (SMF 46642) of *Dasypeltis loveridgei* Mertens, 1954 from Farm Finkenstein near Windhoek, Namibia, showing typical condition of heads shields (top of rostral shield barely evident when viewed from above head; internasals [IN] longer [and often larger overall] than prefrontals [PF]; inter-prefrontal sulcus poorly marked; and frontal shield moderately pitted). (Photo: Joseph Vargas)

each with 5 [2,3] (JV 8646), 7/6 [2,3] (NMWN 2301), 7 [2,3,4] (NMWN 2303), and 7 [2,3,4] / 6 [3,4] (NMWN 235) ($n = 103$). Temporal formula on either side of head usually 2 (anterior) + 3 (posterior) or 2+4: anterior temporals usually two on either side of head (88.3%), occa-

sionally two on one side and three on the other (6.8%), three (2.9%), one (NHMUK 1938.4.7.20), or one left and two right (NMWN 2304) ($n = 103$); posterior temporals three on either side of head (53.4%), 3/4 (20.4%), four (17.5%), four on the one side and five on the other (5.8%), 5/3 (NMWN 1463), 3/2 (NMWN 2288b), and two (ZMB 20983) ($n = 103$). Nasal shield semi-divided (i.e., suture present between nostril and first supralabial) in 90.5% of specimens, entirely undivided in 3.2% (e.g., TM 28147), semi-divided on one side of the head and undivided on the other in 3.2%, semi-divided on one side and fully divided (suture above and below nostril) on the other in ZMB 20983, fully divided on both sides of the head in ZMB 20984, and undivided on the left and fragmentary on the right in NMWN 9585b ($n = 95$). Internasal scales longer (and often larger overall) than prefrontals in 58.9% of specimens, equal in length in 25.6%, longer than prefrontal on one side and equal on the other in 2.2%, prefrontals longer in 12.2%, prefrontal longer on the left and shorter on the right in NMWN 2288b ($n = 90$). When the head is viewed from above, the top of the rostral shield is barely visible in 93.1% of specimens, but distinct in 6.9% ($n = 87$). Midbody scale rows 22–27 ($n = 101$), in males 22–25 (mean 23.4 ± 0.78 , $n = 39$), in females 23–27 (mean 24.2 ± 0.97 , $n = 35$). Ventrals 202–237 ($n = 102$), in males 202–226 (mean 214.3 ± 5.38 , $n = 40$), in females 212–236 (mean 225.7 ± 6.25 , $n = 36$). Subcaudals 38–60 ($n = 100$), 47–60 in males (mean 52.7 ± 3.00 , $n = 41$), 38–50 in females (mean 45.2 ± 2.80 , $n = 34$).

Relative tail length: SVL/tail length in males 4.74–7.10 (mean 5.89 ± 0.54 , $n = 38$), in females 6.33–9.26 (mean 7.42 ± 0.55 , $n = 35$); total length/tail length in males 5.74–8.10 (mean 6.89 ± 0.54 , $n = 38$), in females 7.33–10.26 (mean 8.42 ± 0.55 , $n = 35$).

Size. Largest male (ZMB 5754 – Otjimbingwe) $445 + 75 = 520$ mm; largest female (JV 8646 – Uis) $689 + 91 = 780$ mm.

Localities and material examined. Between Arandis and Usakos – JV 8510; Augustfelde 42, Luderitz district – TMP 52749 (2616CB); De Waal farm – TMP 28147 (2318BD); Finkenstein farm, Windhoek – NMWN 2278, 2304, SMF 46642 (2217CB); Gembokwater, Namib Naukluft Park – TMP 55690 (2215DC); Goageb, 2 km W of – JV 7338 (2617CA); Gobabis – ZMB 20923, 20983–4, 20858a–b (2218BD); Haribes NW 18, near Gibeon – NMWN 2277 (2417DC); Ja Dennoch, Kehoro Suid – NMWN 3189c (2318CA); Kalkrand, Rehoboth – NMWN 2282, 2291 (2417BA); Karibib – NMWN 2297–8 (2115DD); Karibib, 42.3 km W of, on B2 route – JV 7448 (2115CD); Klein Spitzkoppe 70, Karibib district – TMP 42300 (2115CC); Klein Windhoek – SMF 19446 (2217CA); Kuibis, 5.5 km due NW of – JV 7304 (2616DB); Lichtenstein farm near Windhoek – ZMB 44052, ZMH R02273 (2217CA), ZMB 27648 (2217CC); Maltahohe, 37 km due W of – JV 7344 (2416DC); Mari-

ental, 30 km S of – TMP 49876 (2417DD); Mariental–Rehoboth – NMZB 10913; M’bela 200, Rehoboth – NMWN 2300, 2302–3 (2317DD); ‘Namibia’ – FMNH 57654, ZMB 21530; Nauchas farm, Rehoboth Gebiet – NMWN 10132 (2316CB); Neudamm, E of Windhoek – NMWN 2296 (2217CB); Nunib farm, E of Stampriet – TMP 30499 (2418BA); Okahandja – FMNH 64487, NHMUK 1938.4.7.20, NMWN 2289, SMF 46372, TMP 39515 (2116DD); Okahandja, 19 km N of, on B1 route – NMWN 6883 (2116DD); Okanjati farm, Kalkveld – NMW 9963–3 [one specimen] (2016CB); Okapehwe farm near Okasise, Okahandja district – ZMH R02274 (2116DC); Okasise, Okahandja – TMP 29834 (2116DD); Okaukuejo Camp, Etosha National Park – NMWN 9585a–b (1915BB); Okosongomingo 149, Otjwarengo district – NMWN 6828a (2017CA); Omaruru River – TMP 33499 (2214AA); Omaruru, 17.5 km S of, on C33 route – JV 7446 (2115DB); Otjimbingwe – ZMB 5754, 33670a–b (2216AC); Otjozondju 36, Karibib district – NMWN 8255 (2216AA); Paulienenhof farm – ZMH R02289 (2217CB); Plateau 38, Luderitz district – NMWN 2279a–b (2616BC), TMP 48337–9 (2616CB); Rehoboth – NMWN 2280 (2317AC); Rentes 783 – NMWN 235 (1917CB); Scheidthof 293, Windhoek district – NMWN 1828 (2218CA); Seeis, Windhoek district – TMP 58046, ZMH R02270 (2217BC); Springbok Gate, Skeleton Coast National Park – NMWN 7791 (2014AA); Sukses – SMF 46373 (2016DD); Swakopmund, 77 km due NE of – JV 7405 (2215AC); Swakopmund, 90 km NE of, on B2 route – JV 8930 (2215AA); Swakopmund, 96 km due NE of – JV 7407 (2215AA); Twilight 113, Mariental district – NMWN 2305, TMP 42963 (2417BB), NMWN 1463 (2417BD); Uis – JV 8646 (2114BB); Uis Mine, Omaruru district – TMP 54333 (2114BB); Usakos, Karibib – TMP 25810–1 (2115DC); Usakos, near – MRAC 94-041-R-0002 (2115AA); Valencia 42, Rehoboth – NMWN 2288a–b, TMP 35605 (2316AB); Voigtsgrund farm, 49 km due E of Maltahohe – JV 7340 (2417CD); Windhoek – NMWN 2283–6, 2295, 2299, 2301, 3429, SMF 40873, 41928, 46370, 49617, ZMB 20920, 20982 (2217CA); Windhoek, Mandume Ndemufayo Avenue [Gamsberg Road] – NMW 35792 (2217CA); Windhoek, Olympia suburb – NMWN 4509 (2217CA); Windhoek, Pioneers Park – NMWN 238 (2217CA); Windhoek, 0.1 km past steel bridge [Avis] – NMWN 9567 (2217CA); Windhoek, 14 km E of – NMWN 9208 (2217CA); Windhoek and Okahandja, between – ZMB 20921; Zabis 153, Grootfontein district – NMWN 5299 (1917DC).

Dasypeltis cf. *loveridgei*: Kaoko Otavi – NMWN 1465 (1813BC); Karasburg, 5 km NNW of – TMP 54997 (2718DC); Karasburg, 11 km due ENE of – JV 7317 (2818BB); Keetmanshoop, W of – CAS 173379 (2618CA); Mickburg farm, NNE of Grunau – TMP 54996 (2718CB); Orumana, Ohopoho – NMWN 2306 (1813BD).

Distribution. Widespread in Namibia, especially in areas above 1000 m a.s.l., but excluded from the Namib Desert in the west of the country, as well as Woodland and most of the Shrubland-Woodland Mosaic in the north-eastern parts of the country (Fig. 5). Found in the following regions of Namibia: Kunene, Oshikoto, Erongo, Otjozondjupa, Omaheke, Khomas, Hardap, and Karas.

Sympatric with *D. scabra* at the following localities: Windhoek (2217CA), Okahandja (2116DD) and Ja Dennoch (2318CA), and parapatric in several areas throughout the country. The two species also occur together at Etosha Pan (*D. loveridgei*: Okaukuejo camp, *D. scabra*: ‘Etosha Pan’), but the locality details for *D. scabra* are too coarse to plot in Fig. 5.

Conservation. Using IUCN (2022) criteria, this species is considered Least Concern as it is widespread and apparently common, and there are no known major threats to it.

Remarks. FitzSimons’ (1962) record of a ‘Transvaal Museum’ specimen of *D. s. loveridgei* from Tsumkwe in north-eastern Namibia (plotted at 1920BC on his map 32, p. 178), probably in reference to TMP 25091, is referable to *D. scabra*. This specimen and four others from the same locality (see Appendix I) had the typical ‘5N’ *D. scabra* dorsal colour pattern and supralabial formula of 7 [3,4] (but 8 [4,5] on the right side in NMWN 4397).

Photographs of Elzen’s (1980) ZFMK 5426 from Ombujomatamba (Jagd Farm), south of the Waterberg range, were examined and confirm that the specimen is a *D. loveridgei* (weakly constricted hourglass-shaped saddles on back; supralabial formula 5 [2,3] left, 6 [2,3] right; frontal marginally pitted). Elzen (1980) also recorded *D. s. loveridgei* from Okaukuejo (camp) in Etosha National Park, but did not provide a photograph or other evidence (it is not in the ZFMK collection according to M. Flecks, pers. comm., July 2022); and this is an area where both *D. scabra* and *D. loveridgei* may occur (see Fig. 5).

Göthel (2015b) did not provide supporting data for his contention that *D. loveridgei* differs from other *Dasypeltis* by the fine markings on its head. Marais (2022) noted that *D. loveridgei* can be distinguished from *D. scabra* only by having six upper labials, and red colouration. He failed to mention any differences in dorsal markings (e.g., ‘5N’ versus ‘6N’) and *D. loveridgei* is not always ‘red’ (or even reddish-brown).

Key to the genus *Dasypeltis* in Namibia

Dorsal markings in the form of dark brown squarish, rectangular, oval or irregular saddles; belly usually with at least two rows of dark markings on sides; usually 7 supralabials (3rd and 4th contacting orbital); prefrontals usually longer (and larger overall) than internasals; top of rostral clearly visible when head is viewed from

above; frontal usually largely to extensively pitted; inter-prefrontal sulcus moderate or (usually) deep .. *D. scabra*

Dorsal markings in the form of dark brown to reddish-brown hourglass-shaped saddles (deeply to moderately constricted anteriorly and posteriorly); belly usually with single row of small dark markings at edges; usually 6 supralabials (2nd and 3rd contacting the orbital); prefrontals usually shorter (and often smaller overall) than internasals; top of rostral usually barely visible when head is viewed from above; frontal usually smooth to moderately pitted; inter-prefrontal sulcus weakly marked or moderate *D. loveridgei*

MULTIVARIATE ANALYSIS

A total of 110 specimens (30 *D. scabra*: 10 males, 14 females, 6 unsexed; 72 *D. loveridgei*: 24 males, 31 females, 17 unsexed; eight *D. confusa*: at least one male, but ZMH R08914 is probably also a male based on its low ventral and high subcaudal counts, and six females) had complete sets of data and were used in the discriminant function analysis. Three variables (postoculars,

anterior temporals, posterior temporals) of the 13 exhibited little variation and were excluded from the model. In the analysis, 98.2% of specimens were correctly classified, including all *D. confusa*, 96.7% of *D. scabra* and 98.6% of *D. loveridgei* (Table 1). The only specimen of *D. loveridgei* misclassified (as *D. scabra*) was NMWN 9567, which unusually had the prefrontals longer than the internasals and the rostral distinctly visible from above; while one specimen (NMWN 9228) of *D. scabra* atypically had a marginally pitted frontal (State 1) and a weak inter-prefrontal sulcus and was misclassified as a *D. confusa*. *Dasypeltis loveridgei* was for the most part distinguished from *D. scabra* and *D. confusa* along axis 1, on which number of subcaudals (-0.93), the ratio total length/tail length (-0.83), prominence of the rostral scale (-0.67) and number of sublabials (-0.57) loaded most heavily; while *D. loveridgei* and *D. scabra* were for the most part distinguished from *D. confusa* along axis 2, on which subcaudals (1.51), total length/tail length (0.89) and depth of inter-prefrontal sulcus (-0.51) loaded most heavily (Fig. 12, Table 2).

Table 1. Observed (rows) and predicted (columns) classifications of *Dasypeltis* (*D. scabra*, *D. loveridgei*) from Namibia and *D. confusa* from Angola and south-western Democratic Republic of the Congo according to the discriminant function analysis.

	% correct	<i>D. scabra</i> 0.273	<i>D. loveridgei</i> 0.655	<i>D. confusa</i> 0.073
<i>Dasypeltis scabra</i>	96.7	29	0	1
<i>Dasypeltis loveridgei</i>	98.6	1	71	0
<i>Dasypeltis confusa</i>	100	0	0	8
Total	98.2	30	71	9

Table 2. Standardised coefficients for canonical variables in the discriminant function analysis of *Dasypeltis* (*D. scabra*, *D. loveridgei*) from Namibia and *D. confusa* from Angola and south-western Democratic Republic of the Congo.

	Function 1	Function 2
rostral	-0.666154	-0.019163
inter-prefrontal sulcus	-0.234152	-0.508741
sublabials	-0.572065	0.020463
subcaudals	-0.928391	1.509666
total length/tail length	-0.829819	0.891548
internasal/prefrontal	0.364874	0.166350
midbody scale rows	-0.268441	0.083595
preoculars	0.024294	0.343310
ventrals	0.156361	0.321922
frontal	-0.031251	-0.200775
eigenvalue	9.600167	1.322523
cumulative proportion	0.878920	1.000000

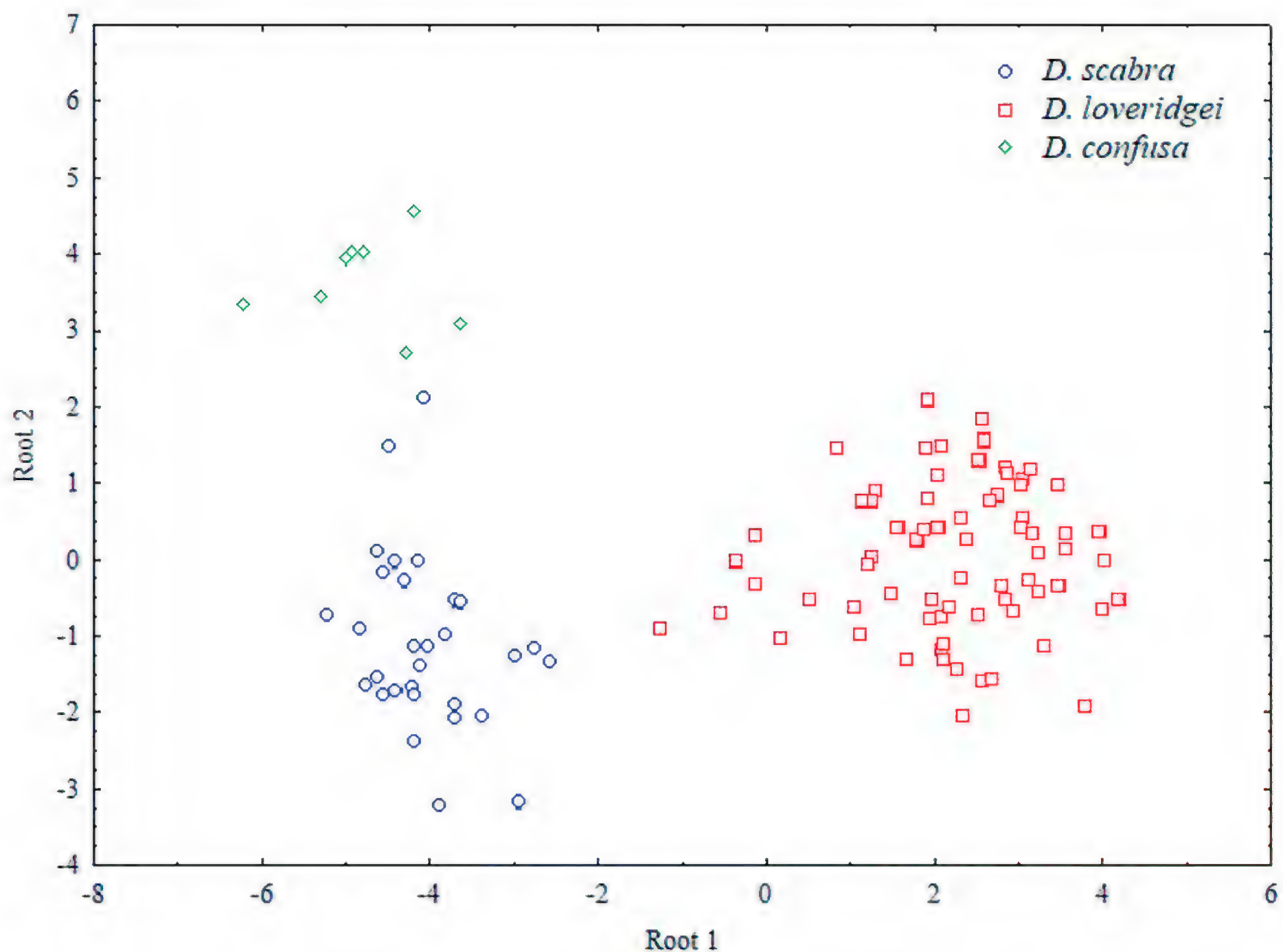


Fig. 12. Discriminant function analysis of *Dasypeltis scabra* and *D. loveridgei* from Namibia, and *D. confusa* from Angola and south-western Democratic Republic of the Congo.

DISCUSSION

Mertens' (1954) description of *D. s. loveridgei* provided only two supposedly diagnostic characters, namely the possession of hourglass-like markings on the back, and a suggestion that the new taxon had greater numbers of ventral plates than typical *D. scabra*. In *D. loveridgei* the saddles are in the form of an hourglass, often with the interspace between saddles similar in size to the saddles themselves, whereas in *D. scabra* the saddles are square, rectangular, oval, and/or a variety of other, often irregular, shapes, and the interspaces between them are usually smaller than the saddles themselves. Also, in Namibian *D. scabra* the colour is never reddish-brown as in some populations of *D. loveridgei* (e.g., Fig. 8).

Gans (1959) noted that Mertens (1954) had essentially named a new subspecies on the basis of its dorsal pattern. Although he treated *D. s. loveridgei* as a synonym of *D. scabra*, Gans (1959) did in fact recognise its unique dorsal pattern, naming it '6N'. He listed several Namibian *Dasypeltis* specimens that fitted the '6N' pattern, and noted (p. 117) that: "There is a reduction in the frequency of [the supralabial formula] 6(2,3) proceeding northward

within southwest Africa, with the three specimens [actually two] from the Waterberg plateau and the Mossamedes [SW Angola] record having 7(3,4) pattern." Gans (1959, appendix 1) listed 33 specimens of Namibian *Dasypeltis* with positive data for numbers of supralabials as well as dorsal colour pattern. Of these, only 10 snakes (from at least five localities) had the supralabial formula 7 [3,4] on at least one side (usually both sides) of the head, and of these, three also had the '5N' dorsal pattern (i.e., *D. scabra*). Instead of looking for a correlation between dorsal colour pattern and supralabial formula, Gans (1959) appears to have simply analysed all Namibian *Dasypeltis* together. Had he excluded the specimens with '5N' patterns, the correlation between '6N' dorsal pattern and 6 [2,3] supralabial formula (i.e., indicative of *D. loveridgei*) would have been more evident (see below).

FitzSimons (1962) later recorded *D. s. loveridgei* from Namibia and noted that its colour pattern (shape of saddles and lateral markings) differed markedly from *D. s. scabra*. Although he emphasised that *D. s. loveridgei* had lower numbers of dorsal saddles (42–54), the present study indicated that there is considerable overlap in this

character between the two species and it does not appear to be diagnostic (36–65, mean 47.3, in *D. loveridgei* versus 41–66, mean 51.7, in *D. scabra*). Broadley (1983, 1990), using a larger sample, subsequently noted a lack of correlation between dorsal colour pattern and characters such as supralabials, ventrals and subcaudals.

However, the present study determined that there was indeed a strong correlation between colour pattern and supralabial formula in both morphotypes. In *D. scabra* 85.4% of the sample ($n = 48$) had the typical *D. scabra* dorsal pattern ('5N') of dark oval, squarish, rectangular or irregular-shaped saddles usually with elongate lateral markings, as well as the supralabial formula 7 [3,4] on at least one side of the head (91.8% [$n = 49$] had the typical *D. scabra* dorsal pattern, and 91.8% [$n = 49$] had the supralabial formula 7 [3,4] on at least one side), whereas in *D. loveridgei* 87.4% ($n = 103$) had the typical *D. loveridgei* dorsal pattern ('6N') of hourglass-shaped saddles usually with squarish to irregular lateral markings, as well as the supralabial formula 6 [2,3] on at least one side of the head (97.1% [$n = 104$] had the typical *D. loveridgei* dorsal pattern, and 90.3% [$n = 103$] had the supralabial formula 6 [2,3] on at least one side). In a few cases the colour pattern assigned to a specimen did not match its species assignment ('5N' for *D. scabra* and '6N' for *D. loveridgei*). For example, JV 95149 is considered *D. scabra* although it has a weakly '6N'-like pattern, but for this specimen and other such cases, the majority of morphological characters were *D. scabra*-like. The same applied to specimens of *D. loveridgei* with '5N' or intermediate ('5N/6N') patterns.

Regarding colour pattern, it has been suggested that *D. loveridgei* is a mimic of the horned adder *Bitis caudalis* (A. Smith, 1839), a thick-bodied viperid snake with a similar dorsal pattern (Branch 1998; Broadley 1983, 1990; Dobiey & Vogel 2007; FitzSimons 1962; Mertens 1954, 1955; Sternfeld 1908, 1910a-c; Werner 1902). In Namibia the distribution ranges of these two species overlap almost entirely (see Fig. 5 for *D. loveridgei*, and maps on p. 116 in Branch 1998 and p. 110 of Dobiey & Vogel 2007 for *B. caudalis*). The resemblance in dorsal markings between the two species, which also both have strongly keeled dorsal scales, can be quite remarkable (e.g., Branch 1998: pl. 13 figs 1, 3; Clauss & Clauss 2002: 89). Both *D. loveridgei* and the horned adder are absent from the north-eastern parts of the country where only *D. scabra* occurs; and the species that the latter has been said to mimic, the common night adder *Causus rhombeatus* (Lichtenstein, 1823), occurs in the vicinity of the Caprivi in the north-east of Namibia (see Fig. 5; and maps in Branch 1998, Broadley 1990 and Dobiey & Vogel 2007).

Two of Mertens' (1954) paratypes of *D. s. loveridgei* were listed as follows: "♂♀ Senck. Mus. Nr. 46371-72. Okahandja, Südwesafrika; W. Hoesch 1.1952." In his monograph on the amphibians and reptiles of South

West Africa, Mertens (1955) noted that one of the *D. s. loveridgei* paratypes (SMF 46372, female, Okahandja) had dorsal markings more similar to those of typical *D. scabra*, leading him to wonder whether its locality information was correct. It can be confirmed that one of the paratypes, a female, shown in Fig. 13 where it bears the label SMF 46371, does indeed have the '5N' dorsal pattern, as well as other features typical of *D. scabra* such as the supralabial formula 7 [3,4], prefrontals longer than internasals, rostral clearly visible from above, and two rows of dark spots at the edges of the venter. This is clearly the same specimen referred to by Mertens (1954, 1955) and Gans (1959) as SMF 46372. The two specimens were collected at Okahandja and their details were recorded on the same label (Fig. 13) at the Senckenberg Museum, Frankfurt. Confusion as to which specimen was which may have resulted if the specimens did not previously have individual labels, but it could also be due to the labels being inadvertently switched, presumably after 1959. Several specimens of both species have in fact been collected in and around Okahandja in central Namibia (see lists of localities), and the two species also occur sympatrically at two other localities in that general area, namely Windhoek and Ja Dennoch, and parapatrically in several additional areas throughout the country (Fig. 5). Surprisingly, although *D. scabra* is quite widespread in the east of Namibia and in the Caprivi region, it was not recorded from the country by Mertens (1954, 1955).

The present study also confirms differences in ventral colour pattern. FitzSimons (1962) had referred to the 'uniformly' white underparts of *D. loveridgei* versus underparts with dark markings, especially at the edges, in *D. scabra*. Close inspection indicated that in 97.0% ($n = 66$) of *D. loveridgei* there are actually small dark markings on the lateral edges of at least some ventrals, forming vague rows (usually one) on either side of the belly, while in comparison, *D. scabra* usually has more extensive dark markings including, in most cases, at least two rows on either side of the belly. While as much as 97.0% ($n = 66$) of the *D. loveridgei* sample had immaculate or weakly marked (single row of dark markings at the extreme edges) bellies, as much as 84.6% ($n = 26$) of *D. scabra* had well marked bellies (two or three rows of dark markings on either side, sometimes with additional scattered dark markings elsewhere on the belly).

FitzSimons (1962) had suggested that *D. s. loveridgei* was smaller than the typical form, growing to 663 mm in total length (585 mm snout-to-vent + 78 mm tail), and later stated that it did not exceed 75 cm in (total) length (FitzSimons 1974). A larger female specimen (689 + 91 = 780 mm) of *D. loveridgei* was examined in this study, but this is still smaller than the largest Namibian *D. scabra*, a female measuring 730 + 97 = 827 mm (another female had a SVL of 773 mm). The largest males in the present study measured 445 + 75 = 520 mm (*D. loveridgei*)



Fig. 13. Paratypes of *Dasypeltis loveridgei* Mertens, 1954 (SMF 46372 left, SMF 46371 right) from Okahandja, north of Windhoek, Namibia. SMF 46372 is a typical *D. loveridgei*, but SMF 46371 is a *D. scabra*. (Photo: Sebastian Lotzkat)

versus $467 + 98 = 565$ mm (*D. scabra*). Elsewhere in its range, *D. scabra* may attain an even greater size (e.g., female from Kenya: $867 + 95 = 962$ mm, see Bates & Broadley 2018). It therefore seems that *D. loveridgei* is indeed a slightly smaller species than *D. scabra*.

Regarding relative length of the tail, FitzSimons (1962) noted that it had been suggested that tail length of *D. loveridgei* was, on average, shorter than that of typical *D. scabra*. The present study indicated considerable overlap in values when comparing total length/tail length in males and females of each species (*D. loveridgei*: males 5.74–8.10, mean 6.89, females 7.33–10.26, mean 8.42; *D. scabra*: males 5.69–6.76, mean 6.25, females 6.93–9.12, mean 8.23), and this is therefore not a reliable character for distinguishing between them. There was also considerable overlap in ventral, subcaudal and mid-

body scale counts, so these are also not, independently, especially useful characters for separating the two morphotypes.

The present study also examined a few characters not previously considered useful for separating the two taxa in Namibia. Frontal shield: usually smooth to moderately pitted in *D. loveridgei* versus usually largely to extensively pitted in *D. scabra*; inter-prefrontal sulcus: shallow to moderate versus usually deep respectively; prefrontal: usually shorter than internasal versus usually longer; and rostral: top of scale usually only barely visible from above versus almost always distinct.

This analysis indicates that *D. scabra* occurs in the Woodland and Shrubland-Woodland Mosaic of north-eastern Namibia, extending into the higher-lying central parts of the country, with a single record in the

south-west which may be associated with populations extending northwards from the Northern Cape Province of South Africa (see Bates et al. 2014; Broadley 1990). *Dasypeltis loveridgei* is widespread in the country but largely restricted to higher-lying areas mainly above 1000 m a.s.l. As noted above, the two species are sympatric at a few localities in central Namibia, and parapatric in several areas throughout the country. It should be noted that Goethel's (2015a,b) concept of *D. loveridgei* is somewhat confused. His map (Goethel 2015a) indicates that this species occurs only in south-western Namibia (i.e., excluding the type locality in the central part of the country) and a small part of the adjacent Northern Cape Province of South Africa, but he later (Goethel 2015b) states that it ranges northwards across Namibia to south-western Angola and may also occur in the South African provinces of Free State, Gauteng and North West.

The use of only one primary line of evidence (e.g., morphology) for distinguishing between species can be problematic especially when differences are small, and an integrative taxonomic approach using multiple lines of evidence is always preferable. However, the present study determined several largely consistent morphological differences between the two species. Therefore, using morphological characters (see Table 3) as operational criteria for species delimitation, together with the occurrence of the two morphs in sympatry in at least a few areas and allopatry in several areas (Fig. 5), with no obvious hybrids/intermediates, it is concluded that two species are present in Namibia, namely *D. scabra* and *D. loveridgei*. The correlation between dorsal pattern ('5N' for *D. scabra* and '6N' for *D. loveridgei*) and morphological characters is largely supported by the discriminant function analysis (Fig. 12, Tables 1–2).

Populations in southern Namibia and the Northern Cape Province of South Africa, as well as north-western Namibia and south-western Angola, with similarities to *D. loveridgei*, are currently being investigated as part of a study on the taxonomic status of *Dasypeltis* in the western half of southern Africa that involves both a molecular phylogeny and an analysis of morphological traits (Bates et al. in prep.).

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Table 3. Comparative morphological data for *Dasypeltis scabra* and *D. loveridgei* in Namibia. Asterisks indicate characters useful for distinguishing between the two species.

	<i>Dasypeltis scabra</i>		<i>Dasypeltis loveridgei</i>	
*dorsal pattern	‘5N’ in 91.8% <i>n</i> = 49		‘6N’ in 97.1% <i>n</i> = 104	
pattern cycles on back	41–66 51.7 ± 4.83 <i>n</i> = 47		36–65 47.3 ± 5.37 <i>n</i> = 99	
*dark markings on belly	2–3 rows on either side, or extensively marked, in 84.6% <i>n</i> = 26		0–1 rows on either side in 97.0% <i>n</i> = 66	
maximum size (snout-vent length + tail length)	♂ 467 SVL + 98 mm tail (TMP 39329) <i>n</i> = 15 ♀ 730 + 97 mm (NMWN 2292); 773 mm (NMWN 253) <i>n</i> = 21		♂ 445 + 75 mm (ZMB 5754) <i>n</i> = 38 ♀ 689 + 91 mm (JV 8646) <i>n</i> = 36	
*supralabials	7 [3,4] in 85.7% <i>n</i> = 49		6 [2,3] in 81.6% <i>n</i> = 103	
*length of prefrontal compared to internasal	PF > IN in 90.5% <i>n</i> = 42		IN ≥ PF in 84.4% <i>n</i> = 90	
*rostral visible from above	Distinct in 97.6% <i>n</i> = 42		Barely visible in 93.1% <i>n</i> = 87	
*frontal texture	Largely to extensively pitted (States 3–4) in 76.6% <i>n</i> = 47		Smooth to moderately pitted (States 0–2) in 68.3% <i>n</i> = 101	
*sulcus between prefrontals	Deep in 68.1% <i>n</i> = 47		Shallow to moderate in 98.0% <i>n</i> = 102	
total length/tail length	♂ 5.69–6.76 6.25 ± 0.38 <i>n</i> = 14	♀ 6.93–9.12 8.23 ± 0.66 <i>n</i> = 19	♂ 5.74–8.10 6.89 ± 0.54 <i>n</i> = 38	♀ 7.33–10.26 8.42 ± 0.55 <i>n</i> = 35
ventrals	♂ 204–220 210.0 ± 4.36 <i>n</i> = 15	♀ 212–240 224.3 ± 6.72 <i>n</i> = 22	♂ 202–226 214.3 ± 5.38 <i>n</i> = 40	♀ 212–236 225.7 ± 6.25 <i>n</i> = 36
subcaudals	♂ 51–62 56.6 ± 3.32 <i>n</i> = 14	♀ 41–55 48.3 ± 3.61 <i>n</i> = 21	♂ 47–60 52.7 ± 3.00 <i>n</i> = 41	♀ 38–50 45.2 ± 2.80 <i>n</i> = 34
midbody scale rows	♂ 22–26 24.1 ± 1.28 <i>n</i> = 15	♀ 23–28 24.8 ± 1.15 <i>n</i> = 23	♂ 22–25 23.4 ± 0.78 <i>n</i> = 39	♀ 23–27 24.2 ± 0.97 <i>n</i> = 35

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APPENDIX I

(*electronic supplement, available at www.zoologicalbulletin.de*)

Appendix I. Size, scalation and colour pattern data for *Dasypeltis* from Namibia. Values in bold refer to characters examined/determined by the author. In some cases most or all data was obtained from Mertens (1954, superscripted 1), Gans (superscripted 2) and D. G. Broadley (superscripted 3). In a few cases most characters were determined by the author, but some values were taken from Gans (1954, underlined) and Broadley (italicised). Values separated by a forward slash refer to left and right sides of the head, respectively. Abbreviations: Y = yes (i.e., deep), F = fair (i.e., moderate), N = no (i.e., shallow), SD = semi-divided, Und = undivided, Div = divided, fragm. = fragmented, IN = internasal, PF = prefrontal, + in column AA indicates extensive markings elsewhere on belly.